On the Bioeconomics of Marine Reserves when Dispersal Evolves

Emily A. Moberg

Biology Department, MS #34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543

Esther Shyu

Biology Department, MS #34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543

Guillermo E. Herrera

Department of Economics, Bowdoin College, 9700 College Station, Brunswick, ME 04011

Suzanne Lenhart

Mathematics Department, University of Tennessee, Knoxville, TN 37996-1300

Yuan Lou

Institute for Mathematical Sciences, Renmin University of China, Beijing, 100872, PRC and

Department of Mathematics, Ohio State University, 231 W 18th Ave, MW 450, Columbus, OH 43210

Michael G. Neubert*

Biology Department, MS #34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543

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*Corresponding author: mneubert@whoi.edu

Abstract

Marine reserves are an increasingly used and potentially contentious tool in fisheries management. Depending upon the way that individuals move, no-take marine reserves can be necessary for maximizing equilibrium rent in some simple mathematical models. The implementation of no-take marine reserves often generates a redistribution of fishing effort in space. This redistribution of effort, in turn, produces sharp spatial gradients in mortality rates for the targeted stock. Using a two-patch model, we show that the existence of such gradients is a sufficient condition for the evolution of an evolutionarily stable conditional dispersal strategy. Thus, the dispersal strategy of the fish depends upon the harvesting strategy of the manager and vice versa. We find that an evolutionarily stable optimal harvesting strategy (ESOHS)—one which maximizes equilibrium rent given that fish disperse in an evolutionarily stable manner—never includes a no-take marine reserve. This strategy is economically unstable in the short run because a manager can generate more rent by disregarding the possibility of dispersal evolution. Simulations of a stochastic evolutionary process suggest that such a short-run, myopic strategy performs poorly compared to the ESOHS over the long run, however, as it generates rent that is lower on average and higher in variability.

Keywords: *evolution of dispersal, evolutionarily stable strategy, fisheries management, marine protected areas, optimal harvesting.*

1 Introduction

No-take marine reserves are a type of "marine protected area" in which fishing is prohibited. Closed areas like marine reserves have been used to manage artisanal fisheries on small spatial scales for many years (Fogarty et al., 2000). The advent of geographical positioning systems (which make the possibility of enforcing closures more feasible (Pala, 2014)) combined with the decline of fish stocks, an increased demand for marine fish protein (FAO Fisheries Department, 2014), and a call for ecosystem-based management, have led not only to increased study of the efficacy of marine reserves but also to an increase in their implementation. Marine protected area coverage worldwide has increased by over 150% since 2003 (Toropova et al., 2010).

A number of studies have shown that marine reserves can contribute to the conservation of stocks and to the ecosystems that support them (e. g., Halpern and Warner, 2002; Halpern, 2003; Lester et al., 2009). Increases in individual size, biomass, population density and species diversity have been shown to increase subsequent to reserve establishment (see examples in, for example, Lester and Halpern, 2008).

The potential economic costs or benefits of reserves are less clear (Kaiser, 2005; White et al., 2008; Hart and Sissenwine, 2009; Fletcher et al., 2015, in press). Some modeling studies (e. g., Neubert, 2003; Sanchirico and Wilen, 2005; Sanchirico et al., 2006; Armstrong, 2007; Neubert and Herrera, 2008; Joshi et al., 2009; Moeller and Neubert, 2013) have shown that the establishment of marine reserves for conservation purposes does not necessarily require a reduction in economic productivity. Indeed, in some models reserves are necessary to maximize yield or sustainable rent. Others (including Polacheck, 1990; Quinn et al., 1993; Man et al., 1995; Holland and Brazee, 1996; Nowlis and Roberts, 1999; Guenette and Pitcher, 1999; Hastings and Botsford, 1999; Li, 2000; Pezzey et al., 2000; Sanchirico and Wilen, 2001; Apostolaki et al., 2002) have shown that reserves may be yield-neutral or produce minor improvements when compared with non spatial effort-control policies. In some cases, the establishment of a reserve decreases yield (Tuck and Possingham, 1994).

The optimality of reserves, then, would seem to depend both on the objective as well as the ecological and economic circumstances. One phenomena, however, emerges from all of these modeling studies, as well as from real-world observations (Fig. 1): the imposition of marine reserves can produce a radical redistribution of fishing effort in space. Effort is displaced from reserve areas

and frequently concentrates near their borders as harvesters attempt to catch the "spillover" from the reserves. As a consequence, the establishment of marine reserves can produce sharp spatial gradients in mortality (Neubert, 2003; Kellner et al., 2007; Joshi et al., 2009; Abbott and Haynie, 2012; Moeller and Neubert, 2013).

It is easy to imagine, that as a result of these gradients, there would be strong selective pressure to evolve context-dependent dispersal (McPeek and Holt, 1992)—that is, low dispersal rates within the reserve and high dispersal rates outside—or, equivalently, the ability for dispersing individuals to detect and preferentially settle in better patches. Since the potential economic benefits of reserves rely on dispersal of individuals from reserves into fished areas, evolution of dispersal might work against the generation of sustainable rent.

In this paper we explore that possibility with the aid of a simple,"two-patch" model (Holt, 1985). We begin by briefly demonstrating that, in the absence of evolution, reserves can be economically optimal when the two patches are sufficiently different in either their biological or economic properties (Sanchirico et al., 2006). We then ask whether reserves are ever optimal (in the sense of maximizing equilibrium rent) when dispersal evolves.

Our analysis of this second problem builds on the work of Law and Grey (1989) and Grey (1993) who were perhaps the first to seriously investigate the interplay between harvest and evolution, i. e., the inclusion of evolutionary change in the constrained optimization problem of the resource manager. They developed the concept of an *evolutionarily stable optimal harvest strategy (ESOHS)*[1]—a harvesting strategy "which gives the greatest sustainable yield, after evolution caused by cropping has taken place." Law and Grey (1989) were particularly concerned with the problem of how age-specific harvesting selects for changes in the age at maturity, so they developed the ESOHS concept in the context of life-history theory (which generally ignores dispersal). We extend their idea here to the evolution of dispersal in a spatially managed fishery and find that evolution qualitatively changes the nature of the optimal distribution of fishing effort.

[1]We prefer the pronunciation *ess-oh-ess* for this acronym.

2 Model

The model we use is similar to those of Clark (1990, pg. 337) and Sanchirico et al. (2006), both of which derive from the classic model of Gordon (1954). The model describes the dynamics of a stock distributed across two spatial locations, or "patches," connected by dispersal. Each patch is characterized by an intrinsic rate of growth r_i and a carrying capacity k_i. Individuals leave a patch at a constant per capita rate m and enter a common pool of dispersers. From this pool a fraction ε (instantaneously) choose to settle into patch 1; the remaining fraction, $1-\varepsilon$, settle in patch 2. In this sense, ε can be thought of as a disperser's preference for patch 1. Patches are harvested at nonnegative patch-dependent effort rates E_i. If the population size of the stock in patch i is x_i, this fishing effort generates yield at the rate $q_i E_i x_i$. The proportionality constants q_i are called the "catchability coefficients."

Under this model, the dynamics of the stock in the two patches are given by the ordinary differential equations

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) - m(1-\varepsilon)x_1 + m\varepsilon x_2 - q_1 E_1 x_1, \tag{1}$$

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{k_2}\right) + m(1-\varepsilon)x_1 - m\varepsilon x_2 - q_2 E_2 x_2. \tag{2}$$

If the price of fish is p, and the cost per unit of effort in patch i is c_i, then the rent generated by harvesting is

$$\pi[E_1, E_2; \varepsilon] = \sum_{i=1}^{2} (p q_i x_i - c_i)\, E_i. \tag{3}$$

At first, we concern ourselves with the case in which a manager is able to control the levels of effort in each of the patches (for example by limiting the number of boat-days available for fishing or by taxing effort) and does so with the objective of maximizing the rent, π, at equilibrium.

It is a simple matter to numerically calculate the equilibrium stock sizes from equations (1) and (2) for any combination of E_1 and E_2. These can be substituted into formula (3) to determine the equilibrium rent. We call the effort levels that maximize the equilibrium rent E_i^*, the corresponding stock sizes x_i^*, and the maximum equilibrium rent π^*.

The optimal solution in patch i will fall into one of three categories depending upon the signs

of E_i^* and the marginal rent in patch i, $pq_i x_i^* - c_i$. If

1. $E_i^* > 0$, we say the patch is *fished*; if

2. $E_i^* = 0$ and $pq_i x_i^* - c_i \leq 0$, we say the patch is *unfished*; and if

3. $E_i^* = 0$ and $pq_i x_i^* - c_i > 0$, we say the patch is in *reserve*.

We distinguish between unfished and reserve patches because the latter would require enforcement by the regulator—an individual harvester would have incentive to fish in that patch, but doing so would reduce the total rent at equilibrium. In unfished patches the marginal rent is negative, and rational harvesters (which we assume) avoid it of their own accord.

The optimal equilibrium effort levels in each patch are determined by the model parameters (Fig. 2). When the patches are economically and ecologically identical, and dispersers settle indifferently (i. e., $\varepsilon = 0.5$), the optimal strategy is to ensure that both patches are harvested at the same rate (or not fished at all if $pq_i k_i - c_i \leq 0$). Asymmetric settlement, or differences in intrinsic growth rates, carrying capacities, or harvest costs can result in the optimal closing of one patch (blue and red regions of Fig. 2). For the rest of the paper, we will explore cases in which patch 1 is in one way (and only one way) better (for the harvesters) than patch 2; that is, all of the inequalities

$$r_1 \geq r_2, \quad k_1 \geq k_2, \quad c_1 \leq c_2, \quad q_1 \geq q_2, \tag{4}$$

are satisfied and only one is satisfied as a strict inequality. This is the case for all of the parameter combinations encompassed by Fig. 2 and subsequent figures.

3 Evolution of dispersal and the ESS

In general, the optimal harvesting effort, and thus the per capita mortality rate, in each patch will differ. The dispersal strategy may evolve in response to this mortality gradient. Evolution, in turn, affects optimal fishing strategies, including the optimality of reserves, through changes in dispersal. Here, we consider the evolution of ε, the proportion of dispersers that settle into patch 1. We derive the evolutionarily stable strategy (ESS), $\hat{\varepsilon}$, the dispersal phenotype against which no alternative phenotype can increase under selection. In this section, we find an expression for $\hat{\varepsilon}$ and

show that it is a "weak form ESS." This ESS is also convergence-stable, making it an evolutionary attractor to which the population will converge in the long run.

3.1 Calculating the ESS

To determine $\hat{\varepsilon}$, we begin by considering a population composed of a single "resident" phenotype with dispersal preference ε. The equilibrium stock sizes, $\bar{x}_1$ and $\bar{x}_2$, satisfy

$$\left[r_1\left(1-\frac{\bar{x}_1}{k_1}\right)-q_1E_1\right]\bar{x}_1-m(1-\varepsilon)\bar{x}_1+m\varepsilon\bar{x}_2=0, \tag{5}$$

$$\left[r_2\left(1-\frac{\bar{x}_2}{k_2}\right)-q_2E_2\right]\bar{x}_2+m(1-\varepsilon)\bar{x}_1-m\varepsilon\bar{x}_2=0. \tag{6}$$

We will find it useful to define α_i as the per capita growth rate, including fishing mortality, in patch i if it were isolated (i. e., if $m=0$). That is,

$$\alpha_i=\left[r_i\left(1-\frac{\bar{x}_i}{k_i}\right)-q_iE_i\right]. \tag{7}$$

α_i can be thought of as the fitness of an individual in patch i at equilibrium.

The phenotype that characterizes the resident population evolves through invasions (and sequential replacement) by rare mutants—alternative phenotypes that appear at low frequencies. Mutants are identical to residents, save for their dispersal preference, which we will denote as ε'. A mutant's fate depends on its *invasion fitness*—its initial growth rate in the resident population. When it first appears, the mutant is rare, and its effect on the resident's population dynamics is negligible (Metz, 2008). Thus if x_1' and x_2' are the mutant populations in the two patches, their dynamics are initially given by the linear system

$$\frac{d}{dt}\begin{pmatrix}x_1'\\x_2'\end{pmatrix}=\mathbf{A}'\begin{pmatrix}x_1'\\x_2'\end{pmatrix} \tag{8}$$

where

$$\mathbf{A}'=\begin{pmatrix}\alpha_1-m(1-\varepsilon') & m\varepsilon'\\ m(1-\varepsilon') & \alpha_2-m\varepsilon'\end{pmatrix}. \tag{9}$$

The invasion fitness is then given by the dominant eigenvalue of $\mathbf{A}'$ (which is always real):

$$\lambda' = \frac{1}{2}\left(\alpha_1 + \alpha_2 - m + \sqrt{(\alpha_1 - \alpha_2)^2 + 2(\alpha_1 - \alpha_2)(2\varepsilon' - 1)m + m^2}\right). \tag{10}$$

Note that the invasion fitness is a function of both the mutant phenotype and the resident phenotype (because the α's depend upon the equilibrium population sizes of the resident, which, in turn depend on ε).

If the invasion fitness (10) is positive, the mutant can replace the resident, inducing evolutionary change; if negative, the mutant will be extirpated. An ESS, $\hat{\varepsilon}$, is a resident phenotype that cannot be replaced by any ε', making it resistant to further evolution (Geritz et al., 1998). A condition that must be satisfied by any ESS is that the selection gradient $d\lambda'/d\varepsilon'$ vanishes when $\varepsilon' = \varepsilon = \hat{\varepsilon}$. Differentiating the invasion fitness (10) with respect to ε' and evaluating at $\varepsilon' = \varepsilon = \hat{\varepsilon}$ gives

$$\left.\frac{\partial \lambda'}{\partial \varepsilon'}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = \frac{(\alpha_1 - \alpha_2)m}{\sqrt{(\alpha_1 - \alpha_2)^2 + 2(\alpha_1 - \alpha_2)(2\hat{\varepsilon} - 1) + m^2}} = 0. \tag{11}$$

Since we have assumed that m is positive, a vanishing selection gradient (11) implies that $\alpha_1 = \alpha_2$; but, adding (5) and (6) we find that

$$\alpha_1 \bar{x}_1 + \alpha_2 \bar{x}_2 = \alpha_1(\bar{x}_1 + \bar{x}_2) = 0. \tag{12}$$

Thus, when the resident population sizes are positive, $\alpha_1 = \alpha_2 = 0$. That is, when the patch preference is at its ESS value, $\hat{\varepsilon}$, the per capita growth rates in the two patches (including fishing mortality) are identical and zero.

By setting $\alpha_1 = \alpha_2 = 0$ in equilibrium equations (5) and (6), we see that the only potential ESS is

$$\hat{\varepsilon} = \frac{\hat{x}_1}{\hat{x}_1 + \hat{x}_2}, \tag{13}$$

where

$$\hat{x}_i = k_i\left(1 - \frac{q_i E_i}{r_i}\right) \tag{14}$$

are the corresponding population sizes.

Substituting the condition $\alpha_1 = \alpha_2 = 0$ into (10), we see that the invasion fitness of any mutant

is 0 whenever the resident phenotype is given by (13). Because the invasion fitness is never positive, no mutant phenotype can increase under selection, confirming that (13) is a local ESS. Because the invasion fitness is always 0, however, every mutant will have the same fitness as the resident, making (13) a 'weak form ESS' (*sensu* Uyenoyama and Bengtsson, 1982).

3.2 Convergence stability of the ESS

As we show next, the evolutionarily stable dispersal strategy (13) is also convergence stable—an evolutionary attractor to which a monomorphic population will converge through small, successive mutations (Geritz et al., 1998). We thus expect the settlement preference to evolve to, and remain at, $\hat{\varepsilon}$.

We demonstrate the convergence stability of $\hat{\varepsilon}$ using the second derivatives of the invasion fitness (10). Convergence stability requires that

$$\left(\frac{\partial^2 \lambda'}{\partial \varepsilon \, \partial \varepsilon'} + \frac{\partial^2 \lambda'}{\partial \varepsilon'^2}\right)\Bigg|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} < 0. \tag{15}$$

That is, the sum of these second derivatives, taken with respect to the resident and mutant phenotypes, must be negative at the ESS $\hat{\varepsilon}$ (Eshel, 1983; Geritz et al., 1998).

Because α_1 and α_2 do not depend on the mutant strategy ε', it follows that $\partial^2\lambda'/\partial\varepsilon'^2 = 0$ when $\alpha_1 = \alpha_2$. Thus, (13) will be a convergence-stable ESS if $\partial^2\lambda'/\partial\varepsilon\,\partial\varepsilon' < 0$ at $\varepsilon' = \varepsilon = \hat{\varepsilon}$.

To calculate $\partial^2\lambda'/\partial\varepsilon\partial\varepsilon'$, first differentiate the invasion fitness (10) with respect to ε':

$$\frac{\partial \lambda'}{\partial \varepsilon'} = \frac{(\alpha_1 - \alpha_2)m}{\sqrt{(\alpha_1-\alpha_2)^2 + 2(\alpha_1-\alpha_2)(2\varepsilon'-1)m + m^2}}. \tag{16}$$

Next, recall that α_1 and α_2 depend on the resident trait ε, and rewrite the equilibrium conditions (5) and (6) as

$$\alpha_1 = m\left[1 - \frac{\varepsilon(\bar{x}_1 + \bar{x}_2)}{\bar{x}_1}\right], \tag{17}$$

$$\alpha_2 = m\left[\varepsilon - \frac{(1-\varepsilon)\bar{x}_1}{\bar{x}_2}\right]. \tag{18}$$

Note that the equilibrium stock sizes $\bar{x}_1$ and $\bar{x}_2$ are both functions of ε.

We can substitute (17) and (18) into (16), and then differentiate with respect to ε to obtain $\partial^2\lambda'/\partial\varepsilon\partial\varepsilon'$. After evaluating the resulting expression at $\varepsilon' = \varepsilon = \hat{\varepsilon}$, as given by (13), we find that

$$\left.\frac{\partial^2\lambda'}{\partial\varepsilon\,\partial\varepsilon'}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = \frac{m}{\hat{x}_1\hat{x}_2}\left[\hat{x}_2\frac{d\bar{x}_1}{d\varepsilon} - \hat{x}_1\frac{d\bar{x}_2}{d\varepsilon} - (\hat{x}_1+\hat{x}_2)^2\right]. \tag{19}$$

The derivatives $d\bar{x}_1/d\varepsilon$ and $d\bar{x}_2/d\varepsilon$ can be found by differentiating the equilibrium equations (5) and (6) with respect to ε. When evaluated at $\varepsilon' = \varepsilon = \hat{\varepsilon}$ and $\bar{x}_i = \hat{x}_i$, as given by (14), these derivatives are

$$\left.\frac{d\bar{x}_1}{d\varepsilon}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = \frac{mk_1r_2\hat{x}_2(\hat{x}_1+\hat{x}_2)^2}{mk_2r_1\hat{x}_1^2 + r_2\hat{x}_2\left[mk_1\hat{x}_2 + r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)\right]}, \tag{20}$$

$$\left.\frac{d\bar{x}_2}{d\varepsilon}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = -\frac{mk_2r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)^2}{mk_2r_1\hat{x}_1^2 + r_2\hat{x}_2\left[mk_1\hat{x}_2 + r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)\right]}. \tag{21}$$

After substituting (20) and (21) into (19), we find that

$$\left.\frac{\partial^2\lambda'}{\partial\varepsilon\,\partial\varepsilon'}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = -\frac{m}{\hat{x}_1\hat{x}_2}\left(\frac{r_1r_2\hat{x}_1\hat{x}_2(\hat{x}_1+\hat{x}_2)^3}{mk_2r_1\hat{x}_1^2 + r_2\hat{x}_2\left[mk_1\hat{x}_2 + r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)\right]}\right) < 0. \tag{22}$$

It follows that inequality (15) is satisfied and the ESS settlement preference (13) is a convergence-stable strategy.

4 The ESOHS and effects of evolution on optimal management

In general, the rent that is generated in each patch depends upon the fishing effort in both patches. This is not the case when the patch preference ε is at its ESS value $\hat{\varepsilon}$, which becomes clear upon substituting the equilibrium stock sizes (14) into the rent (3):

$$\pi[E_1, E_2; \hat{\varepsilon}] = \hat{\pi} = \sum_{i=1}^{2}\left(pq_ik_i\left(1 - \frac{q_iE_i}{r_i}\right) - c_i\right)E_i. \tag{23}$$

This means that when we maximize rent over E_1 and E_2, we are maximizing the rent in the patches independently of each other. Thus, a reserve cannot be part of an ESOHS; a patch should never be closed unless it is unprofitable to harvest (i. e., falls in the 'unfished' category). Specifically, the

ESOHS is

$$\hat{E}_i^* = \begin{cases} \frac{r_i(pq_ik_i - c_i)}{2pq_i^2k_i} & \text{if} \quad pq_ik_i - c_i > 0, \\ 0 & \text{otherwise.} \end{cases} \tag{24}$$

The resulting stock sizes in each patch at the ESOHS are

$$\hat{x}_i^* = \begin{cases} \frac{1}{2}\left(k_i + \frac{c_i}{pq_i}\right) & \text{if} \quad pq_ik_i - c_i > 0, \\ k_i & \text{otherwise.} \end{cases} \tag{25}$$

The evolutionarily stable settlement preference at optimal harvest, $\hat{\varepsilon}^*$, can be calculated using (13) with stock sizes $\hat{x}_i = \hat{x}_i^*$.

Spatial heterogeneity in biological or economic parameters is reflected in the ESOHS (Fig. 3). When the patches differ in their biological parameters (r or k), the ESOHS effort level in the worse patch is smaller than it would be if the patches were identical and the parameter values were equal to their values in the good patch (Fig. 3, first two columns). If the only difference between the patches is due to a difference in intrinsic growth rate (i. e., if $r_2 < r_1$), the ESOHS settlement preference, $\hat{\varepsilon}^*$, remains 1/2, and the stock sizes are equal to one half of the (identical) carrying capacity in each patch. In contrast, when the carrying capacities of the two patches differ (i. e., $k_2 < k_1$), $\hat{\varepsilon} > 1/2$, and settlement in patch 1 is more frequent than settlement in patch 2. In combination with the lower carrying capacity, this dispersal asymmetry results in a smaller equilibrium stock size in patch 2.

When the patches differ in one of their economic parameters (either c or q; Fig. 3, last two columns), $\hat{\varepsilon}^* < 1/2$; that is, settlement is more frequent in the economically poorer patch. If the patches only differ in the cost of fishing (i. e., $c_2 > c_1$), then the ESOHS effort in the more expensive patch, as expected, is lower than in the less expensive patch. Combined with the settlement asymmetry, this results in a larger standing stock in the poorer patch. Similarly, there is a larger standing stock in patch 2 when fish are harder to catch there (i. e., $q_2 < q_1$). In contrast with differences in cost, however, the ESOHS effort level in the patch with lower catchability ($\hat{E}_2^*$) is higher than it is in the patch where fish are easier to catch (at least until fish become so difficult to catch that it is no longer worth harvesting in patch 2 at all).

4.1 Management with reserves

Marine reserves may be part of an economically optimal, equilibrium management strategy when dispersal does not evolve; however, as (24) shows, this is not the case when dispersal does evolve. While marine reserves are not part of the ESOHS, they may be desirable for other purposes. It is therefore interesting to know how the establishment of a reserve would impact profits. The impact of a reserve is contingent upon whether the organisms evolve in response to differences in growth or mortality conditions.

We placed either patch 1 or patch 2 in reserve and calculated the unconstrained rent-maximizing level of effort in the other patch. We also calculated the effort level when the resulting settlement preference was constrained to be evolutionarily stable. We found that using reserves when the settlement preference ε evolves can produce dramatically lower profits (Fig. 4). When a patch is placed in reserve, ε evolves to increase the tendency of fish to disperse to that patch (i.e., when patch 1 is in reserve, ε increases relative to its value when both efforts are optimized to the ESS settlement preference). At least for the parameter values we studied, ε varies most with variation in k_2 and varies least with r_2 (Fig. 4, top row).

4.2 Is the ESOHS economically stable?

The ESOHS represents the best equilibrium harvesting strategy under the constraint that the strategy will not produce further evolutionary change. At the ESOHS no mutant phenotypes can invade and displace the resident phenotype. We have assumed that those mutants are rare, so that there will generally be a long time between mutation events. In between such events, however, the ESOHS is suboptimal. More rent could be extracted from the resource if the manager were to set the effort levels at their *unconstrained* levels (i. e., $\pi[\hat{E}_1^*, \hat{E}_2^*; \hat{\varepsilon}^*] \leq \pi[E_1^*, E_2^*; \hat{\varepsilon}^*]$), and the manager will be sorely tempted to do so. As a result, we should not expect the ESOHS to be economically stable.

As a consequence of fishing at (short-term) optimal levels, rather than according to the ESOHS, the resident phenotype would no longer be an ESS and would be vulnerable to an invasion by a more fit mutant. Of course the manager could simply change his or her harvesting strategy to optimize the rent given this new phenotype. Because of the way it disperses, the potential profitability of

a new phenotype would likely be different than that of the resident. Imagine that this iterative process—harvesting at rent-maximizing rates, invasion of a new phenotype, adjustment of the harvesting rates, etc.—continued for a long time. At some times the instantaneous rent would be larger than that that could be generated by the ESOHS; in some instances, it would be less.

We simulated this "reactionary" policy by introducing a mutant phenotype according to a Poisson process with rate constant μ. We drew the mutant phenotype ε' from a normal distribution with mean equal to the resident phenotype ε, and standard deviation σ, truncated so that $0 < \varepsilon' < 1$. Whenever a mutant appeared, we computed the invasion fitness (10). If the invasion fitness was positive, we replaced the resident by the mutant phenotype and calculated a new harvesting policy that would maximize equilibrium rent for the new phenotype. (In doing so, we implicitly assume that invasion implies displacement. For sufficiently small mutations, Geritz et al. (2002) have proved that this substitution does occur.)

We show a single realization of such a reactionary harvesting policy in Fig. 5. When the mutant invades, the efforts in each patch, the population levels, and the profits also fluctuate. In the case illustrated, ε tends to be less than the ESOHS ε value, while the effort and population levels tend to be higher than the ESOHS level in patch 1 (blue lines) and lower in patch 2 (orange lines). The rent derived from the reactionary policy tends to be less than the ESOHS rent for this realization.

We simulated this stochastic process for a variety of parameter values to assess the average performance of a reactionary versus ESOHS harvesting policy; we found that the rent generated by the ESOHS always exceeded the average rent generated by reactionary harvesting (Fig. 6, top row). It appears that, on average, harvesting at rates that maximize short-term profits selects for new phenotypes that are inimical to expected long-term sustainable rent. In addition to boosting average rent, using the ESOHS has the additional advantage of reducing (to zero) the variability in profits that would accompany reactionary harvesting (Fig. 6, bottom row). Our simulations suggest that the more different the two patches are, the lower and the more variable are the reactionary rents.

5 Discussion

In a simple two-patch model, we have shown that almost every optimal harvesting strategy is unstable in the face of dispersal evolution. The exception is a unique evolutionarily stable optimal harvesting strategy, or ESOHS, where dispersal, as described by the settlement preference, is a convergence-stable, weak-form ESS. The ESOHS, however, is potentially economically unstable: in the short term, a manager could always generate more rent using a different distribution of effort (sometimes using a reserve), at least until a new phenotype invades. A manager who employs a myopic, reactionary strategy of constantly maximizing equilibrium rent, assuming that the current phenotype will not change, suffers reduced average rent, and higher variation in rent, over long timescales. In the real world, there would be economic and social benefits of a consistent harvest strategy, compared to one that changed unpredictably in response to evolutionary changes.

Marine reserves do not play a role in the ESOHS for the two-patch model. This is because evolution of dispersal acts to equalize fitness between the two patches and push population densities to levels that result in no net movement between them. Without this net movement of individuals, or "spillover," from the reserve patch into the fished patch, reserves only reduce economic benefits. The equilibration of fitness across habitats is the sine qua non of the so-called *ideal free distribution* (Fretwell and Lucas, 1969). Based on our results with the two-patch model, we conjecture that, more generally, marine reserves will never be economically optimal when the dispersal behavior of individuals leads to the ideal free distribution of the population. The evolution of dispersal, however, does not inevitably lead to the ideal free distribution. In particular, the ideal free distribution does not emerge as the result of an evolutionary stable dispersal strategy when the environment has a source-sink structure and is characterized by temporal variability in fitness (Holt and Barfield, 2001; Schreiber, 2012). Describing the ESOHS in such circumstances, if one exists, would be challenging.

Our results, when combined with the results from Baskett et al. (2007), who found that increased fragmentation of a reserve network tended to reduce dispersal distance (i. e., increase local retention), suggests that evolution of dispersal may be an important consideration for spatially managed fisheries. However, our understanding of the likely effects of dispersal evolution on optimal management is still nascent. For example, dispersal may encompass a host of traits, including larval duration, the proportion of offspring which disperse or migrate (à la Baskett et al., 2007;

Dunlop et al., 2009), or adaptive movements of mature individuals (à la Abrams et al., 2012). How reserves impact population sizes and selection pressures will depend on the particular dispersal trait.

Of course, settlement preference is not the only life history trait that may evolve in response to harvesting (Borisov, 1978; Jørgensen et al., 2007; Allendorf et al., 2008; Heino and Dieckmann, 2009). Most other studies have focused on size-selective harvest, evolution of age or size at maturity (Kuparinen and Merilä, 2007) and the consequences (both negative and positive) that such fisheries induced evolution can have on sustainable yield or rent(Law and Grey, 1989; Heino, 1998; Law, 2000; Ratner and Lande, 2001; Eikeset et al., 2013). Intriguingly, it has been suggested that marine reserves might ameliorate the consequences of fisheries induced evolution of such traits (Baskett et al., 2005; Miethe et al., 2010). The ramifications of marine reserves in real evolving systems are likely to be complicated by the simultaneous evolution of multiple traits which may have countervailing effects.

While our study suggests that evolution of dispersal may reduce the efficacy of reserves as a rent-maximizing strategy, our analysis focused on equilibrium management on very long timescales. As Sanchirico et al. (2006) highlighted, solving for the optimal harvest trajectory between two patches through time is much more difficult; different results regarding marine reserve optimality may emerge in this case.

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References

Abbott, J. K. and Haynie, A. C. (2012). What are we protecting? fisher behavior and the unintended consequences of spatial closures as a fishery management tool. *Ecological Applications*, 22(3):762–777.

Abrams, P. A., Ruokolainen, L., Shuter, B. J., and McCann, K. S. (2012). Harvesting creates ecological traps: consequences of invisible mortality risks in predator-prey metacommunities. *Ecology*, 93(2):281–293.

Allendorf, F. W., England, P. R., Luikart, G., Ritchie, P. A., and Ryman, N. (2008). Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution*, 23(6):327–337.

Apostolaki, P., Milner-Gulland, E. J., McAllister, M., and Kirkwood, G. (2002). Modelling the effects of establishing a marine reserve for mobile fish populations. *Canadian Journal of Fisheries and Aquatic SciencesJ. Fish Aquat. Sci.*, 59:405–415.

Armstrong, C. W. (2007). A note on the ecological-economic modelling of marine reserves in fisheries. *Ecological Economics*, 62:242–250.

Baskett, M. L., Levin, S. A., Gaines, S. D., and Dushoff, J. (2005). Marine reserve design and the evolution of size at maturation in harvested fish. *Ecological Applications*, 15(3):882–901.

Baskett, M. L., Weitz, J. S., and Levin, S. A. (2007). The evolution of dispersal in reserve networks. *The American Naturalist*, 170(1):59–78.

Borisov, V. M. (1978). The selectivve effect of fishing on the population structure of species with long life cycle. *Journal of Icthyology*, 18:896–904.

Clark, C. W. (1990). *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. John Wiley and Sons, New York.

Dunlop, Erin, S., Baskett, M. L., Heino, M., and Dieckmann, U. (2009). Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. *Evolutionary Applications*, 2:371–393.

Eikeset, A. M., Richter, A., Dunlop, E. S., Dieckmann, U., and Stenseth, N. C. (2013). Economic repercussions of fisheries-induced evolution. *Proceedings of the National Academy of Sciences of the USA*, 110:12259–12264.

Eshel, I. (1983). Evolutionary and continuous stability. *Journal of Theoretical Biology*, 103:99–111.

FAO Fisheries Department (2014). State of world fisheries and aquaculture (sofia). Technical report, Food and Agriculture Organization of the United Nations.

Fletcher, W. J., Kearney, R. E., Wise, B. S., and Nash, W. J. (2015). Large-scale expansion of no-take closures within the Great Barrier Reef has not enhanced fishery production. *Ecological Applications*, 25:1187–1196.

Fogarty, M., Bohnsack, J., and Dayton, P. (2000). Marine reserves and fishery management. In Sheppard, C., editor, *Seas at the Millennium: An Environmental Evaluation*, pages 283–300. Elsevier.

Fogarty, M. and Murawski, S. A. (2004). Do marine protected areas really work? *Oceanus*, 43(2).

Fretwell, S. D. and Lucas, H. L. J. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19:16–36.

Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A., and Parvinen, K. (2002). Invasion dynamics and attractor inheritance. *Journal of Mathematical Biology*, 44:548–560.

Geritz, S. A. H., Kisdi, E., Meszéna, G., and Metz, J. A. J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12:35–57.

Gordon, H. (1954). The economic theory of a common-property resource: the fishery. *Journal of Political Economy*, 62:124–142.

Grey, D. R. (1993). Evolutionarily stable optimal harvesting strategies. In *The Exploitation of Evolving Resources*, pages 176–186. Springer-Verlag.

Guenette, S. and Pitcher, T. J. (1999). An age-structured model showing the benefits of marine reserves in controlling overexploitation. *Fisheries Research*, 39:295–303.

366 Halpern, B. S. (2003). The impact of marine reserves: do reserves work and does reserve size
367 matter? *Ecological Applications*, 13:S117–S137.

368 Halpern, B. S. and Warner, R. R. (2002). Marine reserves have rapid and lasting effects. *Ecology*
369 *Letters*, 5:361–366.

370 Hart, D. R. and Sissenwine, M. P. (2009). Marine reserve effects on fishery profits: a comment on
371 white et al. (2008). *Ecology Letters*, 12:E9–E11.

372 Hastings, A. and Botsford, L. W. (1999). Equivalence of yield from marine reserves and traditional
373 fisheries management. *Science*, 284:1537–1538.

374 Heino, M. (1998). Management of evolving fish stocks. *Canadian Journal of Fisheries and Aquatic*
375 *Sciences*, 55:1971–1982.

376 Heino, M. and Dieckmann, U. (2009). *Fisheries-induced Evolution*. Wiley Online Library.

377 Holland, D. S. and Brazee, R. J. (1996). Marine reserves for fisheries management. *Mar. Res.*
378 *Econ.*, 11:157–171.

379 Holt, R. D. (1985). Population dynamics in two-patch environments: some anomalous consequences
380 of an optimal habitat distribution. *Theoretical Population Biology*, 28(2):181–208.

381 Holt, R. D. and Barfield, M. (2001). On the relationship between the ideal free distribution and the
382 evolution of dispersal. In Clobert, J., Danchin, E., Dhondt, A. A., and Nichols, J. D., editors,
383 *Dispersal*, pages 83–95. Oxford University Press.

384 Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande,
385 B., Gårdmark, A., Johnston, F., Matsumura, S., et al. (2007). Managing evolving fish stocks.
386 *Science*, 318(5854):1247–1248.

387 Joshi, H. R., Herrera, G. E., Lenhart, S., and Neubert, M. G. (2009). Optimal dynamic harvest of
388 a mobile renewable resource. *Natural Resource Modeling*, 22(2):322–343.

389 Kaiser, M. J. (2005). Are mainre protected areas a red herring or fisheries panacea? *Canadian*
390 *Journal of Fisheries and Aquatic Sciences*, 62:1194–1199.

391 Kellner, J. B., Tetreault, I., Gaines, S. D., and Nisbet, R. M. (2007). Fishing the line near marine
392 reserves in single and multispecies fisheries. *Ecological Applications*, 17(4):1039–1054.

393 Kuparinen, A. and Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends*
394 *in Ecology & Evolution*, 22(12):652–659.

395 Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*,
396 57:659–669.

397 Law, R. and Grey, D. R. (1989). Evolution of yields from populations with age-specific cropping.
398 *Evolutionary Ecology*, 3:343–359.

399 Lester, S. E. and Halpern, B. S. (2008). Biological responses in marine no-take reserves versus
400 partially protected areas. *Marine Ecology Progress Series*, 367:49–56.

401 Lester, S. E., Halpern, B. S., Grorrud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D.,
402 Airamé, S., and Warner, R. R. (2009). Biological effects within no-take marine reserves: a global
403 synthesis. *Marine Ecology Progress Series*, 384:33–46.

404 Li, E. A. L. (2000). Optimum harvesting with marine reserves. *N. Am. J. Fish. Manage.*, 20:882–
405 896.

406 Man, A., Law, R., and Polunin, N. V. C. (1995). Role of marine reserves in recruitment to reef
407 fisheries: A metapopulation model. *Biol. Conserv.*, 71:197–204.

408 McPeek, M. A. and Holt, R. D. (1992). The evolution of dispersal in spatially and temporally
409 varying environments. *American Naturalist*, 140(6):1010–1027.

410 Metz, J. (2008). Fitness. In Jørgensen, S. and Fath, F., editors, *Encyclopedia of Ecology*, pages
411 1599–1612. Elsevier.

412 Miethe, T., Dytham, C., Dieckmann, U., and Pitchford, J. (2010). Marine reserves and the evolu-
413 tionary effects of fishing on size at maturation. *ICES Journal of Marine Science*, 67(3):412–425.

414 Moeller, H. V. and Neubert, M. (2013). Habitat damage, marine reserves, and the value of spatial
415 management. *Ecological Applications*, 23(5):959–971.

Neubert, M. (2003). Marine reserves and optimal harvesting. *Ecology Letters*, 6:843–849.

Neubert, M. and Herrera, G. E. (2008). Triple benefits from spatial resource management. *Theoretical Ecology*, 1:5–12.

Nowlis, J. S. and Roberts, C. M. (1999). Fisheries benefits and optimal design of marine reserves. *Fish. Bull.*, 97:604–616.

Pala, C. (2014). Tracking fishy behavior, from space. *The Atlantic*.

Pezzey, J., Roberts, C. M., and Urdal, B. T. (2000). A simple bioeconomic model of a marine reserve. *Ecol. Econ.*, 33:77–91.

Polacheck, T. (1990). Year around closed areas as a management tool. *Nat. Resource Mod.*, 4:327–354.

Quinn, J. F., Wing, S. R., and Botsford, L. W. (1993). Harvest refugia in marine invertebrate fisheries: Models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Am. Zool.*, 33:537–550.

Ratner, S. and Lande, R. (2001). Demographic and evolutionary responses to selective harvesting in populations with discrete generations. *Ecology*, 82(11):3093–3104.

Sanchirico, J. and Wilen, J. (2001). A bioeconomic model of marine reserve creation. *Journal of Environmental Economics and Management*, 42(3):257–76.

Sanchirico, J. and Wilen, J. (2005). Optimal spatial management of renewable resources: Matching policy scope to ecosystem scale. *Journal of Environmental Economics and Management*, 50:23–46.

Sanchirico, J. N., Malvadkar, U., Hastings, A., and Wilen, J. E. (2006). When are no-take zones an economically optimal fishery management strategy? *Ecological Applications*, 16(5):1643–1659.

Schreiber, S. (2012). The evolution of patch selection in stochastic environments. *American Naturalist*, 180:17–34.

Toropova, C., Meliane, I., Laffoley, D., Matthews, E., and Spalding, M., editors (2010). *Global Ocean Protection: Present Status and Future Possibilities*. IUCN.

Tuck, G. and Possingham, H. (1994). Optimal harvesting strategies for a metapopulation. *Bulletin of Mathematical Biology*, 56(1):107–127.

Uyenoyama, M. and Bengtsson, B. (1982). Towards a genetic theory for the evolution of the sex ratio iii. parental and sibling control of brood investment ratio under partial sib-mating. *Theoretical Population Biology*, 22:43–68.

White, C., Kendall, B. E., Gaines, S., Siegel, D. A., and Costello, C. (2008). Marine reserve effects on fisher profit. *Ecology Letters*, 11:370–379.

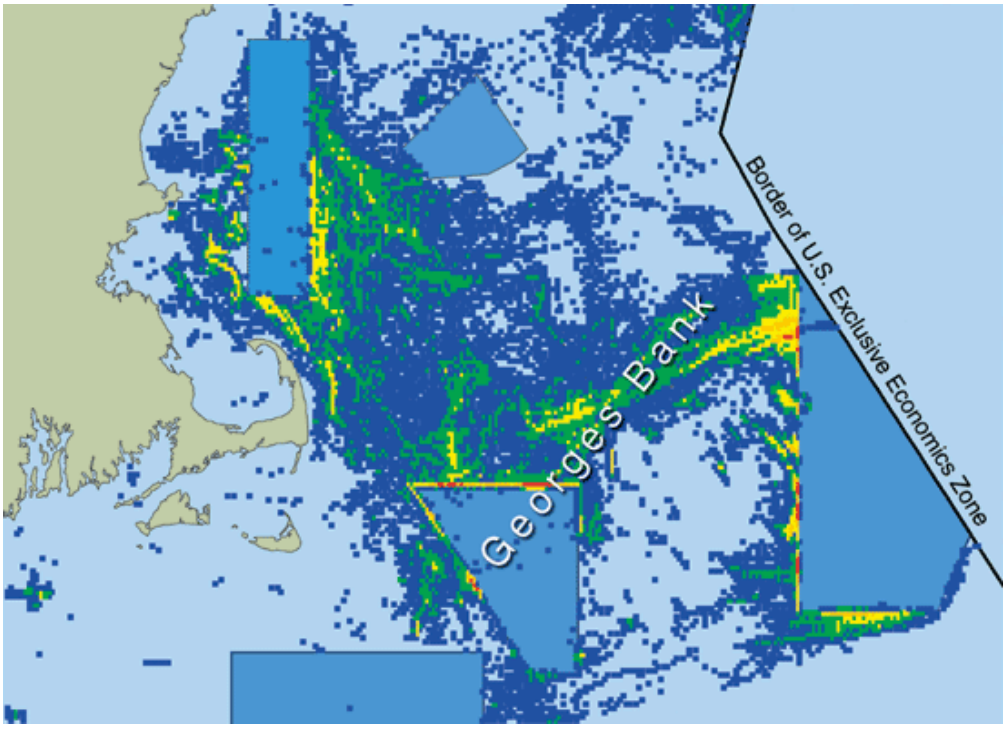

Figure 1: Marine reserves (blue polygons) designed to manage scallop harvest off the New England Coast. Dots indicate estimates of fishing effort in 2003, based on satellite tracking of vessels. Warmer colors (green to red) denote more intense activity. The highest intensity of fishing occurred right at MPA borders. Graphic from Fogarty and Murawski (2004).

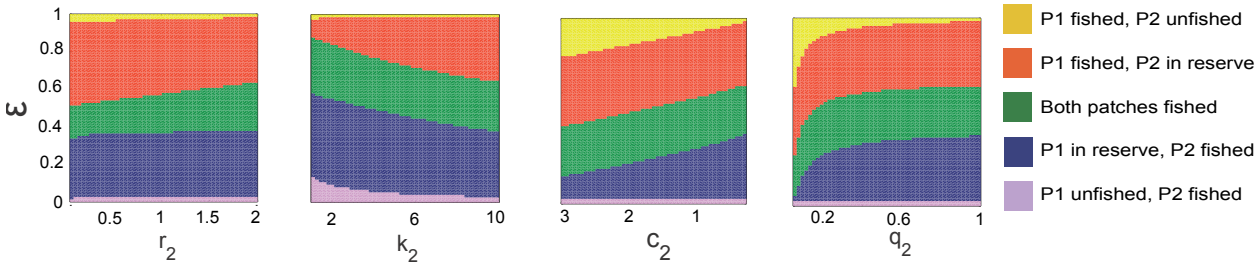

Figure 2: Optimal fishing effort, in the absence of evolution, in each patch as patch 2 quality varies. Patch 2 is the 'poorer' patch in every case, with variations in patch 2 parameters noted on the abscissae. All other parameters are equal between patches, with $k_i = 10, r_i = 2, q_i = 1, c_i = 0.25, m = 4, p = 1$. Note that the axis for c_2 is flipped, because patch 2 becomes 'better' (less costly to fish) as c_2 decreases.

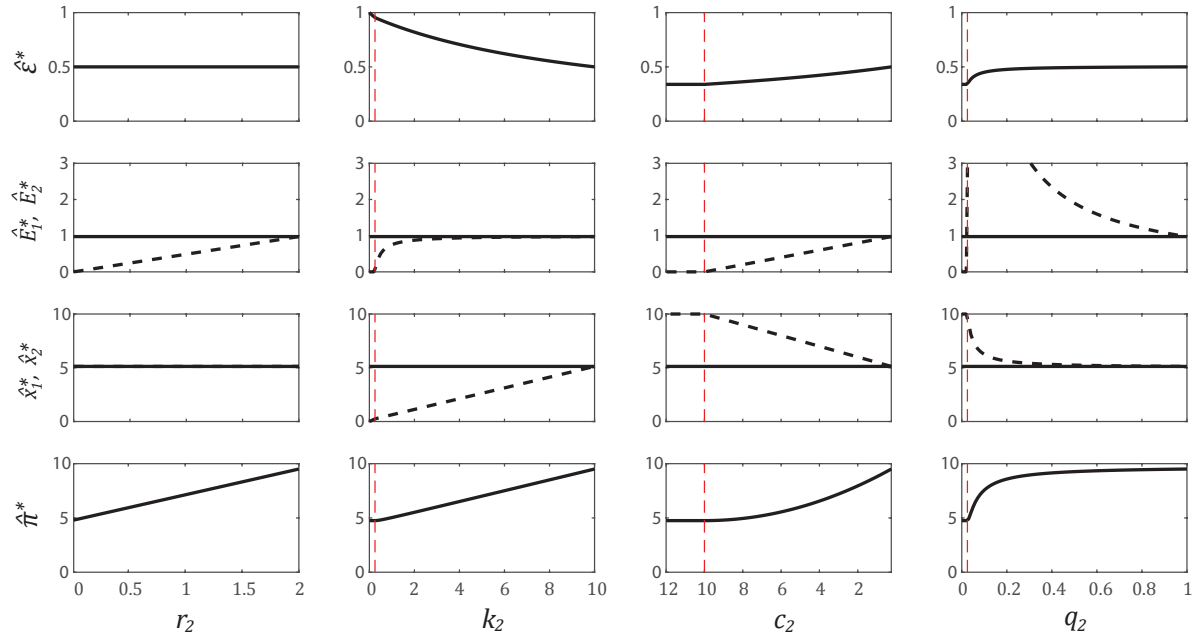

Figure 3: ESOHS settlement preference ($\hat{\varepsilon}^*$), fishing efforts ($\hat{E}_i^*$), stock sizes ($\hat{x}_i^*$) and sustainable rent ($\hat{\pi}^*$). Parameters not plotted are the same as in Fig. 2. In the middle two rows, the solid curves indicate effort or stock size in patch 1; the dashed curves depict the same quantities in patch 2. Note that the abscissa is reversed when it denotes the value of c_2. This makes those figures consistent with the rest in that patch 2 becomes either biologically or economically "worse" as one moves from right to left along the abscissa. Patch 2 is unfished for parameter values to the left of the vertical, red, dashed line in each plot.

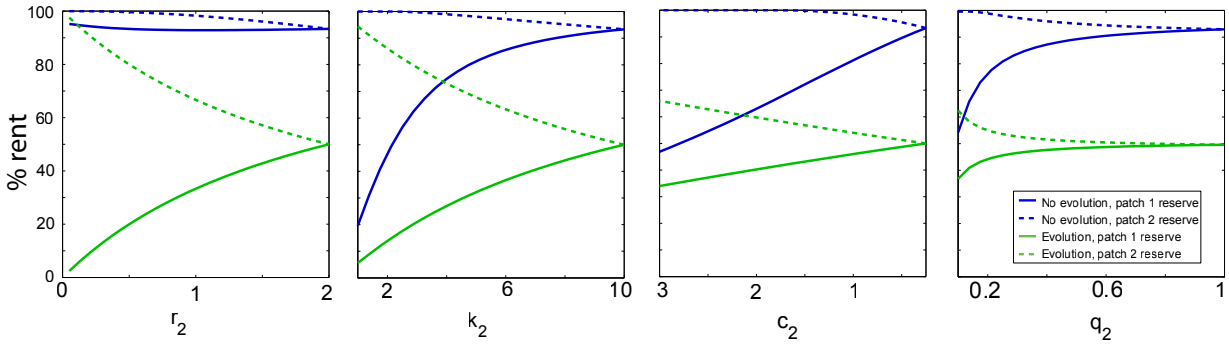

Figure 4: Percent of equilibrium rent lost, relative to an optimally managed system with no evolution (in blue) or with evolution (in green). Either patch 1 is in reserve (solid line) or patch 2 is in reserve (dashed line), and effort in the other patch is managed so as to maximize equilibrium rent. Note that when there is no evolution, closing patch 2 may be part of the optimal management strategy (when the dashed blue line is at 100%). Parameters are the same as in Fig. 2.

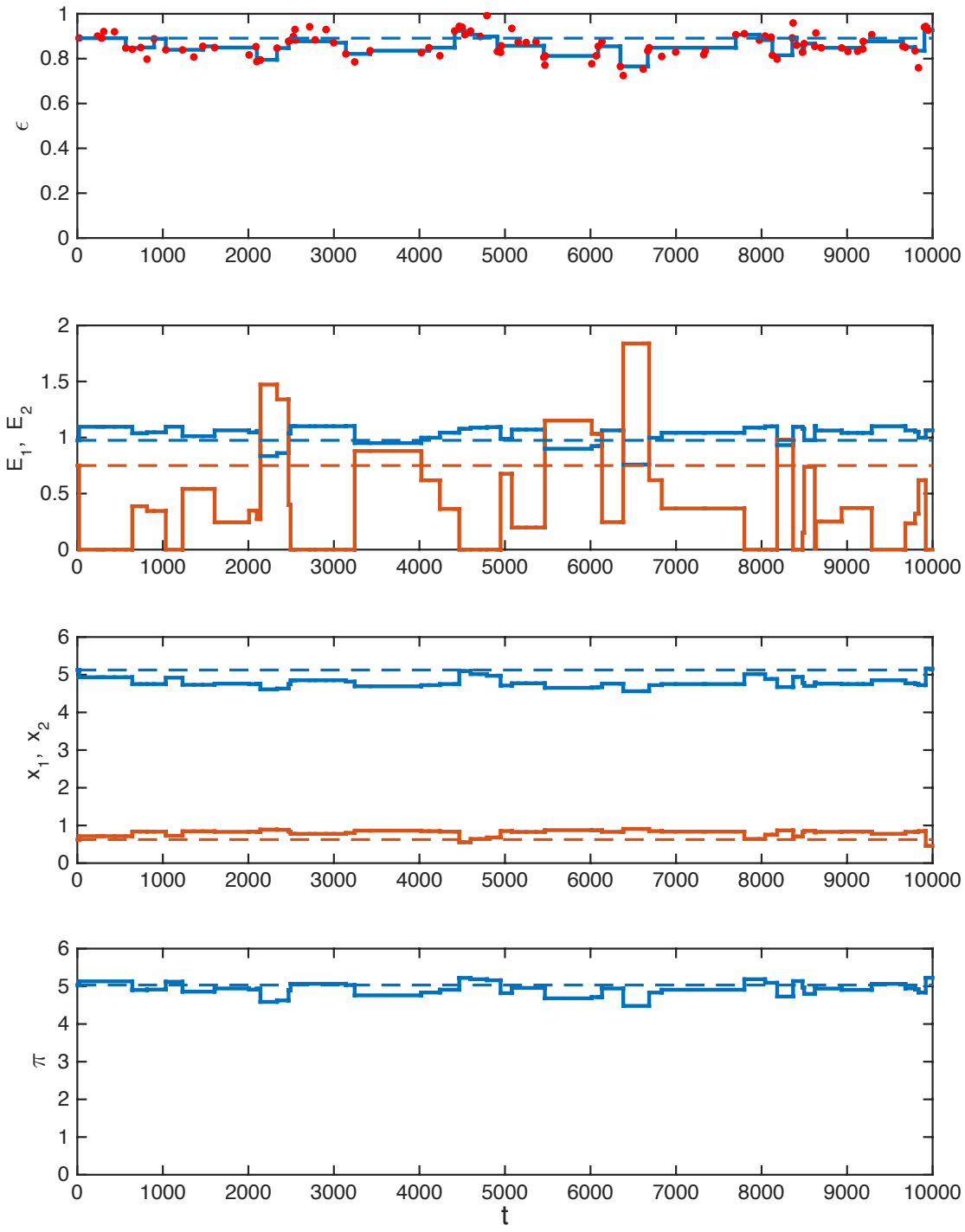

Figure 5: ESOHS harvesting (dotted lines) versus "reactionary" harvesting (solid lines) in which the manager sets effort so as to maximize rent at the current settlement preference (ε) without regard to evolutionary stability. Effort and stock size in patch 1 are shown in blue; in patch 2, orange. Mutants (red dots) appear according to a Poisson process with rate $\mu = 0.01$. Each mutant phenotype ε' is drawn from a normal distribution with mean given by the resident phenotype ε, and standard deviation $\sigma = 0.05$, truncated so that $0 < \varepsilon' < 1$. Parameters are the same as in Fig. 2, except $k_2 = 1$.

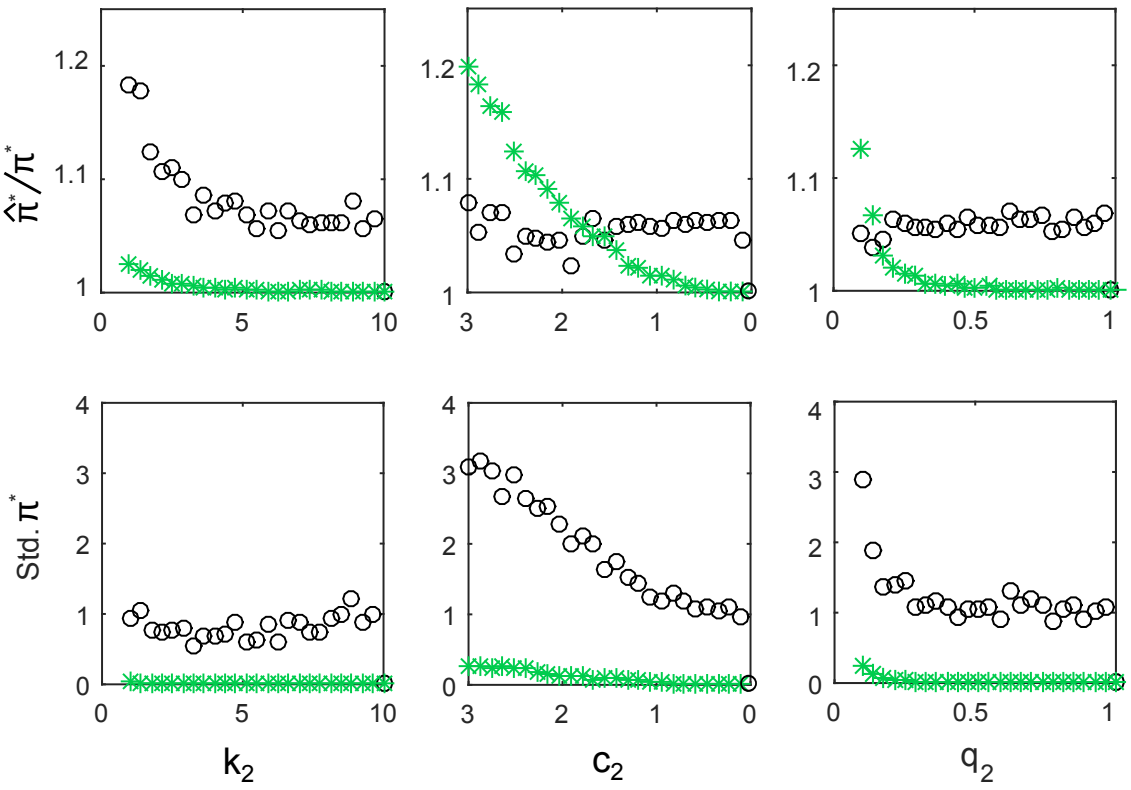

Figure 6: Ratio of average rent (top row) and standard deviation in rent (bottom row) of the ESOHS strategy ($\hat{\pi}^*$) compared to "reactionary" harvesting (π^*) in which the manager sets effort so as to maximize rent at the current settlement preference (ε) without regard to evolutionary stability (cf. Fig. 5). As in earlier figures, all parameters are equal between patches, except that which is noted on the abscissa. Mutants appear according to a Poisson process at the rate $\mu = 0.01$; their phenotype is drawn from a normal distribution with mean given by the resident phenotype, and standard deviation $\sigma = 0.05$ (green stars) or $\sigma = 0.5$ (black circles), truncated so that $0 < \varepsilon' < 1$. Averages were calculated over the time interval [0, 100,000].